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THE ORIGIN OF THE LATERAL OF VERTEBRATES EYES

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THE steps by which the vertebrate sense organs have arisen have been traced in some measure through the evidence afforded by their embryonic growth. In this respect few systems of organs are more homogeneous. It seems to be a well established principle of embryology that all the sense organs of a developing animal shall arise from its outermost layer of cells, the ectoderm, and the fact that sense organs are the chief means by which an animal tests its environment shows that the embryonic source of these organs is not without significance, for what situation is more important for organs adapted to the reception of environmental changes than the outermost surface of the animal that possesses them. These conditions are well illustrated by most of the sense organs possessed by the vertebrates. Our organs of touch have for the most part remained where they were formed in the outermost layer of the skin. The internal ear, which in the great majority of vertebrates is a complicated sac without connections with the skin, is known to arise in individual development as a pocket from the skin secondarily cut off from that layer. Without doubt it is an excessively delicate organ of touch, for hearing and the other sensory activities of the ear seem to be dependent upon the same form of stimulus as touch, except that the kind of stimulus appropriate to the ear is much more refined than that for simple touch. Like the ear, the vertebrate organs of taste and of smell are also probably derived from the skin and in their cases they still retain the primitive connections with the mother layer, for though they are in cavities, these cavities are lined with tissue directly continuous at the mouth of the cavity

with the skin. Thus, excepting the eyes, all the more obvious vertebrate sense organs show immediate and simple relations with the external layer, the skin.

From this standpoint the lateral eyes of the vertebrate are by no means as simple as the other vertebrate sense organs. As has long been known the vertebrate retina, the essential nervous portion of the eye, does not arise directly from the external layer of the animal, but is an outgrowth from the brain. And though the brain arises by involution from the ectoderm and the retina may therefore be said to come directly from that layer, the fact that the retina does not precede the brain in its development but at best differentiates at the same time with the brain, leaves the question of the exact origin of the retina in uncertainty.

Not only is the vertebrate retina, unlike other vertebrate sense organs, not obviously connected with the external ectoderm, but it is also peculiar in the arrangement of its receptive cells, the rod- and cone-cells. In the great majority of sense organs, the receptive mechanism is made up of cells with very marked polarity in that one end of the cell is differentiated as a receiving structure and is directed toward the impinging stimulus, and the other end either tapers into a fibrous process, the nerve fiber, or is in intimate relation with nerve fibers from other cell bodies. In other words, the sense cells are differentiated in that one end serves for reception, and the other for transmission, and the cell is so placed that the receptive end is nearer the source of the stimulus than the transmitting one. In the vertebrate retina this condition is reversed. The light that enters the eye falls first upon the transmitting ends of the sense cells and only after it has passed through these cells does it reach the receptive end. The vertebrate retina is, therefore, appropriately described as an inverted sense organ. Thus the vertebrate eye departs in two important particulars from the other vertebrate sense organs: first, its sensory elements do not arise in any simple or direct way

from the outer ectoderm and, secondly, these elements are inverted in their relation to the stimulus.

As a consequence of these peculiarities of the vertebrate retina numerous theories have been proposed to account for its present condition. It must be quite clear from what has already been stated, that the chances of a simple course of development for the vertebrate retina are not great, and the first theory to be considered emphasizes this feature. This theory was first proposed by Sharp (1885); subsequently it was independently advanced by Béraneck (1890) whose views were supported by v. Kupffer (1894) and especially by Burckhardt (1901). According to this theory the primitive vertebrate retina is what we now recognize as the lens. As is well known, this organ develops as a pocket of ectoderm in the region superficial to the forming eyeball. In its early stages, as v. Kupffer pointed out, it has a striking resemblance to the beginnings of the nose and the ear and its first steps of development recall those of the eyes of many invertebrates. This primitive retina is supposed by the advocates of this theory to be metamorphosed gradually into a dioptric organ and the deeper ganglionic parts are believed to assume receptive functions and thus establish a new retina from tissue that is an outgrowth from the brain. By this process of replacement the primitive retina is converted into a lens and a secondary retina established. It will be observed that while this theory offers an explanation for the lens and for the origin of the retina from a part of the central nervous system, it does not take into account that very striking characteristic of the vertebrate retina, its inversion. Not only is this theory thus defective, but any candid reviewer must agree, I believe, with Keibel that the resemblance that the vertebrate lens has to a sense organ is only of the most superficial kind and that when one attempts to picture the steps whereby a retina is to be converted into a lens and a ganglionic mass into a retina, the difficulties come to be almost insurmountable. For these reasons this theory

has found relatively few advocates and is regarded by many as wholly untenable.

The second general theory, as to the origin of the vertebrate retina, is one which has much more in its favor and which is presented in as complete a form by Balfour (1881) as by any other. It has recently been independently advanced by Jelgersma (1906). According to this view the vertebrate retina originated on the outer surface of the ancestral vertebrate in much the way that the eyes of many invertebrates have been produced. The primitive retinas thus formed were implanted in that portion of the surface of the animal from which the central nervous system was destined to develop and when this was infolded these retinas were carried in with it, and came thus to be involved in the central organ. If the

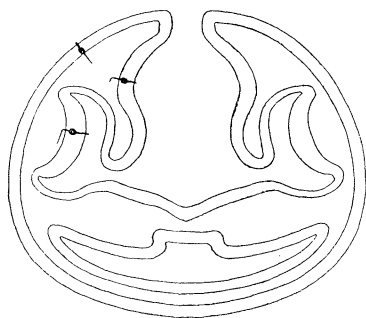


FIG. 1. Imaginary transverse section through the head of a vertebrate embryo to show the morphological relations of the surfaces of the ectoderm of the integument, the medullary tube, and the forming retina. In each of these situations a single sense cell is indicated.

morphological position of a sensory cell such as may have existed in the primitive external retina is supposed to have been retained as this organ was carried from its superficial location into the central nervous system and out again almost to the external surface, the resulting retina would be composed of inverted elements (Fig. 1). Thus this theory at once offers an explanation for the two most striking features of the vertebrate retina, namely, its formation as an apparent outgrowth from the central

nervous system and the inverted condition of its receptive cells.

The most obvious objection to this view is that the retina must be supposed to be a functional organ during this whole process of migration and inversion. But this objection, as others have already pointed out, is not serious, for if we imagine these processes to take place in animals like certain pelagic tunicates or even amphioxus, the transparency of the body would be such as to offer no hindrance whatever to the continuous action of such an organ even when in its deepest position. From this standpoint, therefore, there is no serious objection to the theory as already outlined.

The various adherents of this theory have differed considerably as to the details of its application. The general account of it already given is the particular form which was advocated by Balfour (1881) and which has since been revived by Jelgersma (1906). Balfour makes no mention of any living animal that might be taken to represent, according to this theory, a stage in the evolution of the eye. Von Kennell (1881) designated the annelids as probable ancestors and attempted to show how the external eyes of these worms could be converted into the type of eye found in the vertebrates. Jelgersma on the other hand has accepted amphioxus as an intermediate form and has based his description of the evolution of the eyes on the conditions found in this animal. These three investigators agree in believing that the vertebrate eyes have arisen from optic organs that were once on the exterior of an ancestral form. Lankester (1880) and Boveri (1904), however, do not place the origin of the eye in so remote a region but believed that it arose in the central nervous system in such a place as is now occupied by the eye of the ascidian larva (Lankester) or the numerous eyes of amphioxus (Boveri). In this way these two investigators abandon some very significant parts of the Balfour theory but in other respects they follow it very closely.

Whether we accept the annelids, or amphioxus, or still other animals as representatives of the ancestors of the vertebrates, we shall find it necessary, according to the Balfour theory, to assume some intermediate form in which the eyes are so located as to represent a condition between a primitive integumentary eye and one such as is possessed by the true vertebrates. Such a condition occurs apparently only in the minute larvæ of the ascidians and in amphioxus. As very little is known about the actual conditions in the ascidians in this respect, we shall turn our attention to the optic organs of amphioxus.

Great diversity of opinion has been expressed as to the parts of amphioxus that are sensitive to light. From recent experimental work, however, it may be taken as

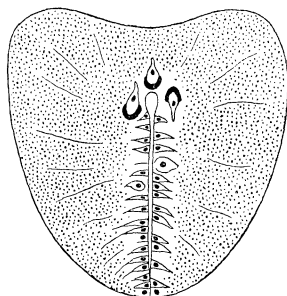


FIG. 2. Transverse section of the nerve tube of amphioxus, showing three direction eyes in place. Modified from Hesse.

fairly well established that the so-called eye-spot at the anterior end of the nerve tube and the integument of amphioxus are not sensitive to light, but that the small pigment cups described by Hesse (1898) as photo-receptive organs and found through almost the whole length of the nerve tube are the true visual organs. They lie in the substance of the nerve tube and though they have not been regarded by Hesse as in any way connected with the vertebrate eyes, they occupy a position that is very suggestive of a stage intermediate between an external eye and one such as the vertebrate now possesses.

Viewed from this standpoint the optic cups of amphioxus are not without interest. They can be seen well in any transverse section of the nerve tube of this animal (Fig. 2) provided the section is not taken from a part of the body too far toward the anterior end. In such a section the cups will be found close to the central canal. Each cup is made up of a concave pigment cell in the hollow of which is a fan-shaped cell. The expanded end of this fan-shaped cell fills the pigment cup while the handle of the fan tapers off into a nerve fiber. The whole structure, as Hesse observed, has a most striking resemblance to the simple direction eye of certain planarians, and it is difficult to resist the conclusion that amphioxus is an animal whose nerve tube is richly provided with a simple type of direction eye.

If these bodies in the nerve tube of amphioxus are direction eyes, their positions are not without significance. On examining a number of transverse sections in which they occur, it will soon be recognized that their arrangement is any thing but regular. Most of them are directed either dorsally or ventrally, but almost any position may be assumed. Though they lie near the central canal, they are not arranged in reference to it with any degree of uniformity. Some point away from it, others toward it.

The lack of uniform arrangement shown by these visual cups is of considerable importance in relation to Balfour's theory of the origin of the retina. If this theory is correct, the inversion of the retina is dependent upon a rigid orientation of the sensory cells which is supposed to have been retained absolutely from their place of origin of these cells in the external skin, through every step in their migration to their final position in the completed retina. If once in the course of this migration orientation is lost, the mechanism fails. Since amphioxus is the only animal that represents well an intermediate stage in this process, and since in amphioxus the orientation *is* lost, it seems to me that Balfour's explanation

falls to the ground. I, therefore, do not believe that the vertebrate retina is inverted because it has been inherited from an integumentary source, and I agree with Boveri that the condition in amphioxus removes all occasion for the assumption that the vertebrate retina arose on the exterior of an ancestral form and became deep-seated by being involved in the developing central nervous system. That the central organs should thus become a seat for the origin of essentially sensory mechanisms is not surprising as long as such an appropriate stimulus as light can in certain cases reach them. Even in our own bodies the respiratory reflex is maintained through the direct stimulation of the medulla by the blood that passes through it, an operation the first step of which must be equivalent to the process of sensory stimulation.

I know of no reason for assuming that the visual apparatus of amphioxus arose in any other than its present position, and I believe there is good grounds, as Boveri has pointed out, for the opinion that the visual cells of amphioxus are the homologues of the rod- and cone-cells of the vertebrates. These visual cells then probably represent the material out of which the vertebrate retina has been made. If this is true why have the eyes of vertebrates developed where they have and how does it come that their retinas are inverted?

An answer to the first of these questions can be found, I believe, in the size of the vertebrate body as compared with that of such an animal as amphioxus. In amphioxus the body is so small and thin that it is sufficiently transparent to allow light to penetrate it anywhere. Hence visual organs may be functional at any point along the length of its nerve tube. In most fishes, however, the increase of size has involved such a development of the body musculature that the posterior part of the nerve tube, the spinal cord, is completely buried in thick, almost opaque tissue. Hence visual cells would no longer be serviceable in such a region as this and they have doubtless thus been restricted to what has become the brain

region of the nerve tube. Furthermore in the brain region the development of the musculature for the gills and jaws together with the growth of the cranium as a support for this musculature must have cut off the light from below. Hence the natural growth of the body of the fish would tend to restrict the occurrence of the visual cells to the sides of the anterior end of the nerve tube, the regions from which the eyes of the vertebrates develop. It is in this partial envelopment of the nerve tube with somewhat opaque tissue that, in my opinion, has limited the eyes of vertebrates to their present positions.

An answer to the second question raised, namely, why is the vertebrate retina inverted, is found, I believe, in the structure of just such direction eyes as amphioxus possesses. The visual cell in each of these eyes has its receptive end buried in the depths of its pigment cup and its fibrous end directed outward through the open mouth of this cup. As the effective light necessarily enters the cup through its mouth, the visual cell is inverted in its relation to this stimulus. If then we imagine a retina to be formed from a great aggregation of individual direction eyes of the type found in amphioxus, it follows that the receptive elements of such a retina would be inverted. This, in my opinion, is the reason for the inversion of the receptive cells in the retina. The vertebrate retina then is fundamentally unlike the other vertebrate sense organs in that it is not directly derived from the external ectoderm, but is developed as a part of the central nervous system, and its inversion is dependent upon its origin from an aggregation of direction eyes each one of which was of necessity inverted from the beginning.